NATURE AND SIGNIFICANCE OF THE EVOLUTIONARY TRENDS OF THE SIPHONOSTOMATOUS CYCLOPOIDES LIVING IN ASSOCIATION WITH ECHINODERMS, WITH NOTES ON *STEPHOPONTIUS TYPICUS* THOMPSON AND SCOTT

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(With 2 text-figures)

CONTENTS

I—INTRODUCTION

Copepods have been found frequently living in association with various other animals. The nature of association varies greatly and ranges from pure, highly degenerate to the simple, relatively unmodified condition. Various terms have been employed to denote this relationship between the copepods and their hosts. "Copepod associates" suggested by Gooding (1957) seems to express the actual relationship better than any other term. It is desired to emphasise, however, that while some groups are still hesitant to depart from their free living existence for a thoroughly associated life, there are other groups which appear to be definitely on tracks towards obligatory parasitism. One such group is constituted by a number of siphonostome cyclopoids living in association with echinoderms. Most of them seem to be incapable of free existence, nor are they found to be associated with other hosts. Further,

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the members of this copepod assemblage share with each other many common characteristics which are not found outside the group.

According to the original definition, the siphonostome cyclopoids formed a coherent group and are characterised by the presence of an oral siphon. However, both Giesbrecht (1899) and Sars (1915) have recognised Cancerillidae as an exception to the rule for in this family the siphon was only feebly developed. Recently some more families (Micropontiidae Gooding, 1957 ; Stellicomitidae Humes & Cressey, 1958 ; Nanaspidae Humes & Cressey, 1959) have been added, whereas in Cancerillidae, the siphon is absent or reduced to a very short extension of the labrum and the labium. The facts that all these forms are associates of echinoderms and that they all share many common features in contrast to the rest of the siphonostomes suggest that the members of these families have taken an altogether separate evolutionary track. This view is necessarily suggestive of an early divergence among siphonostomes and a possible splitting of the latter into two tribes, one tribe with a well-developed siphon and a non-prehensile antenna, and the other with a highly reduced siphon and prehensile antenna.

The family Micropontiidae is monogeneric, containing the genus *Micropontius* Gooding, 1957. The Stellicomitidae contains three genera: *Onycopygus* Humes & Cressey., 1958, *Asterocomes* Rao, 1962, and *Stellicomes* Humes & Cressey, 1958, the first two genera being monotypic. Cancerillidae contains four genera: *Cancerilla* Dalyell, 1851, *Parartotrogus* T. A. Scott, 1893, *Concerillopsis* Stephensen, 1933 and *Ophiopsyllus* stock *et al.* 1963.

Changeux (1958) described a new genus of copepod *Allantogynus* from ophiuroid host and referred it to Cancerillidae, but later on (1960) the same author created a new family Allantogynidae to accomodate it. Bresciani and Lutzen in : Stock *et. al.* (1962) have called attention to the similarities existing between Nanaspidae and Allantogynidae and indicated that the latter is only a synonym of the former. However, there are sufficient differences between *Nanaspis* and *Allantogynus* to retain their separate identities. *Allantogynus* will thus form the second genus of the family Nanaspidae.

There is another interesting genus *Stephopontius* obtained "in the general washings of dredged invertebrates" described by Thompson & Scott (1903). The species has never been reported after its original description. I have now obtained this species from the washings of *Holothuria atra* from the Gulf of Mannar. Humes & Cressey (*loc. cit.*) discussed the possible systematic relationships of this species and indicated that it is related to *Nanaspis*. I am convinced that *Stephopontius* could fit into the definition of the family Nanaspidae as modified by Stock *et al.* (1962). But the differences between the two genera are described in table I.

TABLE I—The differences between *Nanaspis* Humes & Cressey and *Stephopontius* Thompson & Scott

Nanaspis Humes & Cressey	*Stephopontius* Thompson & Scott
Prosome is 2-segmented. First segment is the cephalosome and second segment is the result of fusion of all the four pedigerous segments.	Prosome is 3-segmented. First segment is the cephalothorax formed by the fusion of cephalosome and first pedigerous segment. Second segment is the result of fusion of the succeeding two pedigerous segments. Last segment is the fourth pedigerous segment.
Last segment of prosome does not carry any accessory appendage.	Last segment of prosome carries two pairs of expanded structures, one pair on each side in female ; in male no such appendage is seen.
Urosome in both sexes consists of a leg-bearing first segment and genital segment. Genital segment a sub-rectangular complex.	Urosome is incompletely 2-segmented in female and incompletely 3-segmented in male. First segment carries foliaceous fifth legs. The genital segment carries sixth pair of legs in male.
Geniculate male antennule is 6-jointed.	The geniculate male antennule is 2-jointed.
Exopods of second and third legs are each 3-jointed.	Exopods of second and third legs are each 2-jointed.

Before proceeding further with the phylogenetic relations and the question of speciation in these echinoderm associates, it is desirable to give a brief description of *Stephopontius typicus* Thompson & Scott. The latter authors have presented the salient features of the species. The following notes are supplementary to it.

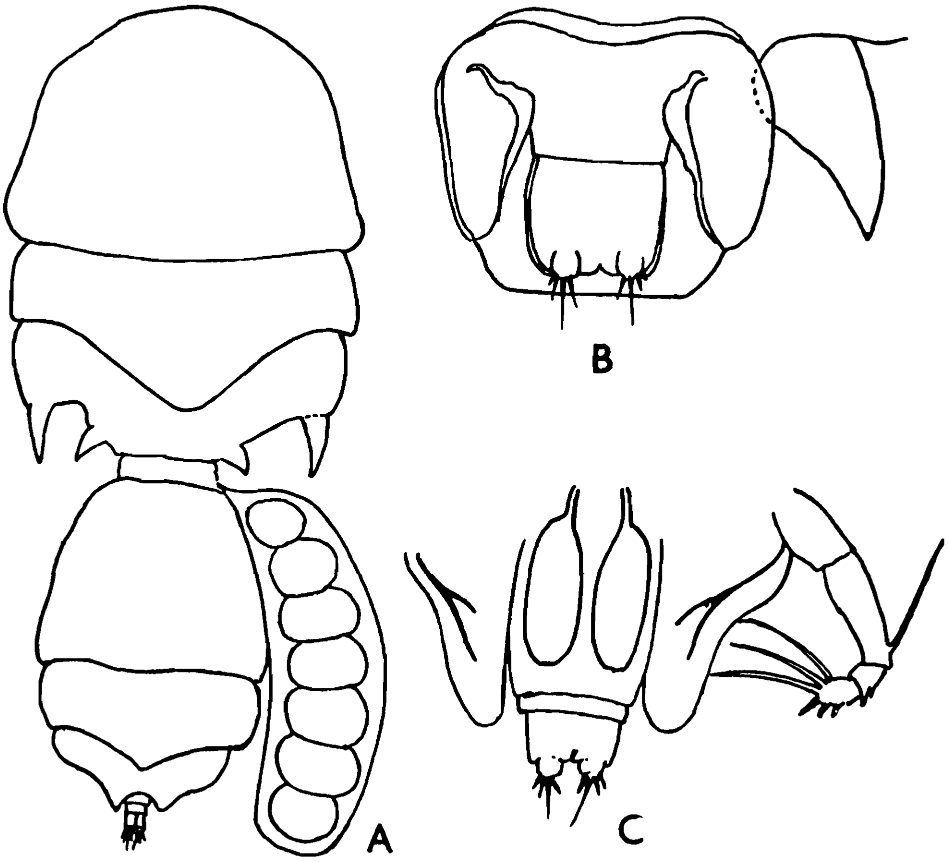
II—DESCRIPTION OF *Stephopontius typicus* THOMPSON & SCOTT

1903. *Stephopontius typicus* Thompson and Scott, p. 203, pl. XX.
1959. *Stephopontius typicus*: Humes and Cressey, p. 212.

One female and two male specimens (one male and female in paired state) were obtained from washings of *Holothuria atra* from the Gulf of Mannar on 15th December 1960.

Thompson & Scott (*loc. cit.*) reported the sizes of the two sexes as 6.0 and 8.0 mm., respectively. This is, as Humes & Cressey have pointed out, obviously a typographical error. In their figures of adult female and male they have given a magnification scale. According to this scale, male is smaller than female, their respective sizes being 0.5 mm. and 0.65 mm. This is the same size range as that of the present examples.

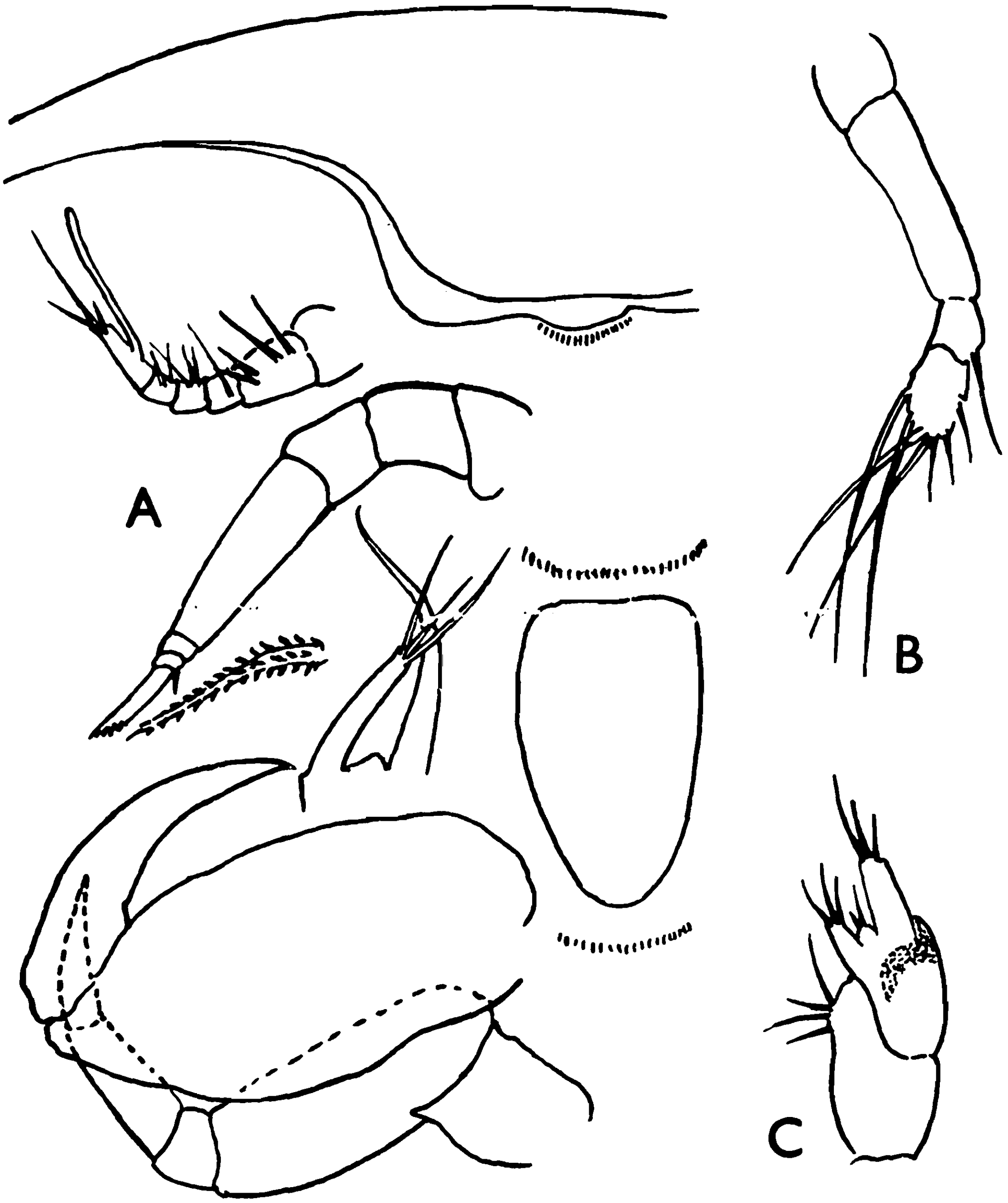
Prosome (Text-fig. 1 A) is 3-segmented. First segment is the cephalothorax, having been formed by fusion of cephalosome and first pedigerous segment. Second segment is the result of fusion of second and third pedigerous segments and bears those legs. Last segment carries fourth pair of legs. An elongated, rather spindle-shaped process is borne on each of the postero-lateral corners of the last prosomal segment. At about the junction of this segment with urosome a pair of foliaceous structures is borne, one on either side (Text-fig. 1 B). They can be compared to the somewhat similar structures found in *Micropontius ovoides*.



TEXT-FIG. 1A. Adult female and male in paired condition. (Only one ovisac is shown in female). B. Female urosome, ventral view. C. Male urosome, ventral view.

There is a pair of egg sacs, each egg sac is cylindrical, a little incurved containing 5-7 eggs, arranged one above the other. The cephalosomal appendages (Text-fig. 2 A) and third leg (Text-fig. 2 B) are figured. The third leg differs from the fourth leg in possessing three spines and four setae on the second exopod segment. Fifth leg is foliaceous and uniarticulate without any accessory process. Urosome is a rectangular mass, with a slight indication of division into two segments. Fifth legs are borne on the antero-lateral corners of the proximal segment. Caudal rami are small sub-spherical structures borne on the posterior side of urosome, one on either side. Each ramus carries four setae which are flattened and non-jointed. These structural details are not seen in dorsal view as they are covered by a flap.

Male differs from female in the smaller size, in the geniculation of the antennule and in the presence of sixth pair of legs. Antennule (Text-fig. 2 C) is a highly modified structure, apparently 2-segmented, but possibly containing more segments. The first segment is simple. carrying three setae on anterior margin ; the second segment is covered



TEXT-FIG. 2A. Ventral view of cephalosome of female showing various appendages. B. Female third leg. C. Male antennule.

by a transparent flap on dorsal side. In ventral view it is seen to terminate in three lobes, all carrying a number of setae. Both segments are highly calcified. Urosome (Text-fig. 1 C) is 3-segmented, the division between first and second segments being indistinct on ventral side. The sixth leg consists of a small rounded lobe, bearing three setae. It is borne on the postero-lateral corners of second urosomal segment. Size: Female 0.66 mm. and male 0.55 mm.

Thompson & Scott (*loc. cit.*) reported this species from the Ceylon Pearl Banks and the present record is the first rediscovery of this species.

III—DISCUSSION

Stock *et. al.* (1963) have discussed a possible relationship between Cancerillidae, Nanaspidae, Stellicomitidae and Micropontiidae. The association of each of these families with different classes of echinoderms is noteworthy; Cancerillidae with ophiuroids, Nanaspidae with holothuroids, Stellicomitidae with asteroids and Micropontiidae with echinoids. Their phylogenetic affinity is all the more supported by the structural gradations that are exhibited by *Asterocomes* Rao whose many characters are "partly shared by some of the genera of the related families, namely *Micropontius* Gooding (Micropontiidae) and *Nanaspis* Humes & Cressey (Nanaspidae)" Rao (*loc. cit.*). The salient features of the four families are compared and contrasted in table II.

Stock *et. al.* (1963) suggested that Micropontiidae "are not closely related to the others, since they exhibit differences in the structure of the first antenna and leg 1." This view, however, cannot be extended too far. A large number of segments in the antennule is also met with in *Asterocomes* Rao. The elongated first endopods could well be considered as specialised development for firmer attachment to the spiny echinoid body. It is interesting to note that *Asterocomes* also shows many semblences to *Nanaspis* like the extreme suppression of swimming legs. It would appear that though the four families constitute four coherent groups, the different genera in these families exhibit many kinships one way or the other. It is likely that the discovery of newer genera would further contribute towards bridging the structural gradations between them. One is more inclined to emphasise the development of those basic characters which are meant for an associated existence with different classes of echinoderms. The important differences between these four families of copepods on the one hand and the rest of the siphonostomes on the other are presented in table III.

In considering the nature and significance of the evolutionary trends of the siphonostomatous cyclopoids living in association with echinoderms following features are noteworthy:

(a) Smaller size;

(b) General reduction of appendages and fusion of body segments;

(c) Prehensile antenna; and

(d) Absence of siphon.

It is not known whether these copepods have any specificity in relation to their hosts, or any special preference for particular area on the host body. The occurrence of *Stellicomes tumidulus* on such widely separated hosts as *Pentaceros hedemanni* (Lutken) in the Gulf of Mannar and *Protoreaster lincki* (Blainville) off Nossi Be, Madagascar probably provides a negative data regarding specificity. Rao (1962) reported the occurrence of *S. tumidulus, S. guineensis* and *Asterocomes indicus* on the same host, *Pentaceros hedemanni*. Also it is likely that they occur anywhere on the host body, including the tube-feet areas and the topographical crevices and elevations found on the surface of the host body. It is understandable that in order to be of greatest adaptation for living in these restricted spaces on the host body the animals should necessarily be very small. The actual size range found in these copepods generally is from 0.30 mm. to 0.60 mm. with the exception of a few species belonging to *Cancerilla* and *Parartotrogus*, and the latter situation is probably the consequence of their frequent free existence.

A streamlined body with as much fusion of different segments of the body as possible would similarly contribute towards a firmer hold on the host body. The circulation of waters around the hosts will pass by a smooth surface, but is likely to create a frictional force on animals with protruding angular edges and points, constantly trying to dislodge them. Accordingly, we find that in all these echinoderm associate copepods, except, again, in some of the Cancerillids caught independently of the host, there is a cohesive fusion of different body segments and there is hardly any distinction between prosome and urosome. Not only is the fusion very complete, but often the body presents very smooth outer surface.

Antennae are quite strongly developed and prehensile. In these copepods the premium has been on the general reduction of appendages, particularly those which aid in swimming and mastication. However, an associated animal, coming to depend more and more on the host, must develop clinging devices and this is actually rendered by the antennae. In fact it is the most powerfully grown organ of the animal. It is articulate and provided with strong claws. Presumably they function for attachment to the host body.

Absence of siphon is another interesting point. Echinoderms are benthic organisms and their movements, if at all, are of a restricted nature. Consequently there is a constant accumulation of decaying organic matter, both settled and excreted, on the external surfaces of the host. In such circumstances there is hardly any need for the copepod associate to develop complex and elongate tubular apparatus for sucking in the food materials which are available in plenty and almost all the time. As a matter of fact none of the species belonging to these four copepod families have any distinctly developed siphon. At the most the labrum and labium get fused to form a circular or oval disc or ridge, the mouth being situated in its center.

The foregoing discussion demonstrates that the siphonostomatous families Cancerillidae, Micropontiidae, Stellicomitidae and Nanaspidae have evolved quite a bit towards 'parasitising' the echinoderms. It must, however, be added that the relation is not strictly parasitism or semiparasitism, for the copepods do not feed at the expense of echinoderms. It may probably be qualified as symbiosis, but how far essential the copepods are to the echinoderms as cleaning agents is not definitely known. None of these copepods have been reared or experimented upon in the laboratory. More informations of biological and ecological nature are required for any definite statement.

As we have already found, after their deviation from the rest of siphonosomes many specialised characters, have been developed in these copepods towards a close associated existence with the echinoderms. However, our knowledge of this copepod group is in an imperfect state and we do not know whether the limited number of species and genera known under different families indicate the real state of affairs or only the insufficiently of our knowledge of these forms. In any case it appears that the relationship of these copepods with their hosts is very intimate and ancient. This view is supported not only by the many characteristic morphological features discussed earlier, but also by the world-wide distribution of some species. *Stellicomes tumudulus* has already been referred to, Another species, *S. guineensis* is recorded from the east Atlantic (off the coast of Cape Sierra Leone) and the northern Indian Ocean (off the south east cost of India) on such widely separated hosts as *Oreaster clavatus* Muller and *Pentaceros hedemanni* (Lutken) respectively. *Micropontius ovoides* Gooding has been recorded from Plymouth, off Mediterranean (Stock, 1960) and off Swedish coasts (Bresciani & Lutzen, 1962) and *M. glaber* Stock *et. al.* which differs only in some structural details from *M. ovoides*, has been recorded from the other side of the Atlantic, off Jamaica.

Within the group the evolutionary changes appear to have been very slow, particularly so for smaller taxonomic categories. Stock *et. al.* (1962) reports: "More than one species of *Nanaspis* may occur in a single locality as seen in the case of *N. poolens* and *N. exigua* both of which were found at Drunkenmans Cay, Jamaica." They added: "It is worth noticing that three *Nanaspis* species (*N. poolens, N. exigua* and *N. media*) may occur on the same species of holothurian, thus raising interesting but as yet unanswerable questions on the nature and causes of speciation in this genus" It is, again, interesting to note that although substantial differences exist between different families and genera, the distinguishing marks between the species are rather insignificant, and there is hardly any variation between individuals at all. One is tempted to say that the evolution within the lower taxonomic categories of this copepod group has been monotonously slow.

IV—SUMMARY

A group of Siphonostome Cyclopoids living in association with Echinoderms and belonging to the families Cancerillidae, Micropontiidae, Stellicomitidae and Nanaspidae are peculiar in that the oral siphon in these forms are highly reduced or altogether absent. Their exclusive association with various classes of Echinoderms coupled with some structural peculiarities point to the possibility of an early divergence of these echinoderm associate copepods from the main evolutionary stem of the siphonostome cyclopoids.

Stephopontius typicus is described for the first time after its original description by Thompson and Scott in 1903. Brief notes are added on the species and its relations are discussed.

V—REFERENCES

BRESCIANI, J. AND LUTZEN, J. *in* : STOCK, *et. al.* 1962. Parasitic copepods from the west coast of Sweden including some new or little known species.—*Dansk. Naturfrerdn.*, Kbenhaven, **124**, pp. 367-408.

CHANGEUX J. P. 1958. Quelques caracters biologiques d'um Copepode parasite d' Holothuries: *Allantogynus delamarie.*—*C. R. Acad. Sci.*, Paris, **247**, pp. 961-964.

CHANGEUX, J. P. 1960. Contribution a l'etude des animaux associes aux Holothuries.—*Actual. Scient. techn.*, Paris, **1248**, p. 124.

GEISBRECHT, W. 1899. Dei Asterocheriden des Golfes von Neapel.—*F. and F. Neapel*, *Fauna flora Golf. Neapel*, Berlin, **25**, pp. 1-217, 11 pls.

GOODING, R. U. 1957. On some copepods from Plymouth mostly associated with invertebrates including three new species.--*J. mar. biol. Ass. U.K.*, Plymouth, **36**, pp. 195-221.

HUMES, A. G. AND CRESSEY, R. F. 1958. A new family containing two new genera of cyclopoid copepods parasitic on star fishes.—*J. Parasit,* Lancaster, 44, pp. 395-408.

HUMES. A. G. AND GRESSEY, R. F. 1959. A new family and genus of cyclopoid copepods parasitic on a holothurian.—*Ibid,* **45,** pp. 209-216.

RAO, C. A. P. 1962. A new genus and species of cyclopid copepod parasitic on a starfish.—*J. mar. biol. Ass. India,* Mandapam Camp, **4** (1), pp. 100-120.

SARS, G. O. 1915. An account of Crustacea of Norway, **6,** 1-221, Bergen (Bergen Museum Publication).

STOCK, J. 1960. Sur quelques Copepodes associes aux Invertebres des cotes du Roussillion.—*Crustaceana,* Leiden, Arabic, **1,** pp. 218-257.

STOCK, J., HUMES, A. G. AND GOODING, R. U. 1963. Copepods associated with West Indian Invertebrates I.—*Stud. Fauna Curcao,* TheHague, **13**, pp. 1-20.

STOCK, J., HUMES, A. G. AND GOODING, R. U. 1962. Copepods associated with West Indian Invertebrates—II.—*Ibid.*, pp. 1-23.

THOMPSON, I. G. AND SCOTT, A. 1903. Report on the Copepoda collected by Prof. Herdman at Ceylon in 1902.—*Rep. Pearl Oyster. Fish Suppl.*, **7**, pp. 227-307.

TABLE II

Salient features of the Families Cancerillidae, Micropontiidae, Stellicomitidae and Nanaspidae

Cancerillidae	Micropontiidae	Stellicomitidae	Nanaspidae
1. Prosome & urosome often distinct with segments clearly marked. Sexual dimorphism well-developed except in *Ophiopsyllus*.	1. Little distinction between prosome and urosome and little flexibility between segments. Sexual dimorphism feebly developed.	1. Little distinction between prosome and urosome and hardly any segmentation. Sexual dimorphism feebly developed.	1. Little distinction between prosome and urosome. Segmentation little developed. Sexual dimorphism feebly developed in *Nanaspis* and strongly developed in *Stephopontius*.
2. Urosome ill-developed short, with varying number of segments.	2. Urosome a single subrectangular complex, bearing fifth legs in the proximal half.	2. Urosome minute, 1-segmented.	2. Urosome 1-segmented in *Nanaspis*. In *Stephopontius* it is 1-segmented in female but 3-segmented in male.
3. Female antennule 6 to 9 segmented. Male antennule 6 to 10 segmented, may or may not be geniculate.	3. Female antennule 14-segmented; male antennule 13-segmented and doubly geniculate.	3. Female antennule 3-or 4-jointed in *Onycopygus* and *Stellicomes* and 14-jointed in *Asterocomes*. No geniculation in male antennule.	3. Female antennule 8-jointed in *Nanaspis*, 6-jointed in *Stephopontius*. Male antennule 5- or 6-jointed in *Nanaspis* and only 2-jointed in *Stephopontius*; in both cases geniculate, weakly.
4. Antenna, prehensile with powerful claw, 3 or 4 segmented. Exopod, when present, very rudimentary.	4. Antenna prehensile, strong, 4-segmented with terminal claw. No exopod.	4. Antennule 4-jointed with terminal claw. No exopod.	4. Antenna prehensile, and 4-jointed in *Nanaspis*; weakly prehensile and 5-jointed in *Stephopontius*.
5. Siphon obsolete.	5. No siphon. Mouth slightly protruding, labrum and labium fused into a flattened structure.	5. The sucking apparatus formed of labrum and labium; shows sexual dimorphism.	5. Sucking apparatus formed of labrum and labium as a flat disc.

(*Contd.*)

TABLE II—*Continued*

Cancerillidae	Micropontiidae	Stellicomitidae	Nanaspidae
6. Mandibles short, extending straight inward, palp absent.	6. Mandible consists of masticatory blade and palp; former protrudes into the mouth through the gaps of the labrolabial complex.	6. Mandible simple spine; adjacent seta is palp.	6. Mandible minute, simple spine; no palp.
7. Outer lobe of maxillule present only in *Parartotrogus* and *Ophiopsyllus*; inner lobe short and stout terminating in 3 setae.	7. Maxillule biramous, rami ending in setae.	7. Maxillule biramous, ramus bearing setae in *Onycopyous* and *Stellicomes*, spine and setae in *Asterocomes*.	7. Maxillule biramous, seta like.
8. Maxilla and maxillipeds of asterocherid type.	8. Maxilla 2-segmented, second segment modified to a strong claw. Maxilliped asterocherid.	8. Maxilla 2-jointed, maxilliped asterochrid type.	8. Maxilla 2-segmented, second segment a claw. Maxilliped of asterocherid type.
9. First to fourth legs showing varying stages of reduction usually of generic significance. Even when best developed (*Parartotrogus* & *Cancerillina*) first leg is more reduced than second leg; fifth leg usually present, rudimentary.	9. First and second legs biramous, each 3-segmented, In third and fourth legs only exopods are present both 3-segmented.	9. Swimming legs biramous, Endopod a single segment. Exopod 3 jointed except in first leg where it is 1 jointed in *Stellicomes* and *Onycopygus* and 2-jointed in *Asterocomes*.	9. First and second legs biramous, rami 1-jointed in the former; in second leg, 3ndopod is 2-segmented; exopod consists of 2 joints in *Stephopontius* and 3 joint in *Nanaspis*. Third and fourth legs uniramous; former consists of 3 joints in *Stephopontius* rami 2-jointed in fourth leg.
10. Caudal rami normal.	10. Caudal rami normal.	10. Caudal rami minute, variable in form.	10. Caudal rami minute with setae.

Table III—The differences between echinoderm associate copepods and other siphonostomatous copepods.

Echinoderm associate copepods	Other siphonostomatous copepods
The group at present contains four families, Cancerillidae, Micropontiidae, Stellicomitidae and Nanaspidae. Live in association with different classes of echinoderms.	Includes all other siphonostomatous cyclopods. Free living or living in loose or close relation with a variety of invertebrates.
Very small, below 1 mm. (with rare exceptions), and mostly below 0.5 mm. Hardly any distinction between prosome and urosome (again with rare exceptions) and segmentation of the body little exhibited.	Usually large in size, with well-developed prosome and urosome. Body segments mostly clearly demarcated.
Female antennule usually 3 to 7 segmented except in *Micropontius* and *Asterocomes* where they are 14-segmented. Male antennule always geniculate and composed of a smaller number of segments.	Female antennule 9-to 21-segmented and fairly large. Male antennule genioulate; in Asterocheridae it consists of smaller number of segments and in Artotrogidae of a larger number of segments than the female antennule. Varying situations are met with in other families.
Antenne prehensile and strongly developed. 3- or 4-segmented. Exopod is absent except in the case of *Parartotrogus* where it is present as a delicate setiferous lamella. Mostly ending in a terminal claw.	Antenna non-prehensile, composed of 4 or 5 joints. Exopod vestigeal in most cases, attached to second endopod segment. Exopod is probably most developed in Acontiophoridae.
Siphon absent. Labrum and labium may just meet making a protrusion.	"Oral parts not adapted for mastication, the anterior and posterior lips being generally produced to form a prominent one termination in long or short siphon" (Sars, loc. cit.)
Mandible and maxillule feebly developed. Maxilla and maxilliped of the asterocherid type.	Mouth parts usually well-developed and adapted for mastication.
Swimming legs exhibiting varying degrees of reduction. Maximum reduction probably in *Asterocomes*. Fifth legs present, but in reduced or modified form. Sixth legs often present in males.	Swimming legs usually well-developed. Normally biramous, rami being 3 jointed. Independant reduction of segments and rami of the legs takes place in different. general and families. (Ummerkutty, 1962, 1966). Fifth legs always present. Sixth legs often present in males,